THE MECHANISM OF EXTENSION IN THE LEGS OF SPIDERS [1]

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INTRODUCTION

Prior to 1909 morphologists studying the leg musculature of spiders unanimously considered movement in each joint to be controlled by antagonistic muscles. The femoro-patellar and tibio-metatarsal joints (the two most important flexor-extensor joints in the leg), however, are not supplied with such paired muscles, since there are no extensor muscles (Petrunkevitch, 1909). The alacrity of extension in these joints, therefore, presents the singular problem of accounting for these "muscle-less" extensor movements.

The assumption has been made by Petrunkevitch (1909, 1916, personal communication 1941) that "the function of extension has been taken over entirely by the elastic interarticular membrane." Except for this single suggestion by Petrunkevitch, no mechanism has been forwarded to account for these forceful and rapid extensor movements. It has seemed worthwhile, therefore, to investigate this problem.

The spiders used in the present study have included the tarantulas, *Dugesiella californica, Delopelma helluo,* and *Aphonopelma cryptethus* representing the suborder Mygalomorphae, and *Agelena naevia* (the grass spider), *Miranda aurantia* (the golden garden spider), *Latrodectus mactans* (the black widow), and *Aranea cavicata* (large orb-weaver) representing the suborder Dipneumonomorphae. All of the specimens were collected in or near Pasadena, California.

With respect to the morphological and functional relationships studied in the present investigation, no significant differences between the species were found.

RESULTS AND DISCUSSION

A. *The possibility of extension by muscular contraction*

That muscular contraction is not the extensor mechanism is obvious. In agreement with Petrunkevitch it has not been possible to find any trace of extensor muscles (see below) in the two joints under consideration. Furthermore, the axis in each of these joints is located dorsally in such a way as to preclude attachment of extensor muscles. At these joints the appendages are flattened over the dorsum in the articular region, and are joined by very narrow dorsal interarticular membranes. During flexion or extension these membranes serve as simple hinges. With this extreme dorsal location of the axis there is no conceivable way in which

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internal muscular attachments could be made whereby muscular contraction would produce extension of the joint, and it is certain that no tendons pass externally over the hinge. Therefore, the theory of muscular extension must be discarded.

B. *The possibility of extension by the interarticular membrane*

There are two interarticular membranes (Fig. 1 dm, vm), one dorsal, the other ventral. Of these the dorsal one is very short. Petrunkevitch (1909) claimed for this dorsal membrane the un-assisted function of extension, but examination of his paper has not given the experimental basis upon which he based this conclusion.

Were the elasticity of this membrane the mechanism involved in extension it would seem imperative that the spider assume a position of complete extension in death. This is not the customary position taken; spiders nearly always die with their legs completely and permanently flexed. In fact, so characteristic is the flexed position in death that when startled a number of spiders assume the position as a protective reflex (Robertson, 1904).

It might be reasoned that this position of extreme flexion is due to an irreversible contracture in the muscles. That such a mechanism is not responsible for this flexed position was shown by the following experiment: A leg was removed at the trochanter and the chitin covering the ventral half of the femur was removed, due care being taken to leave both the ventral and dorsal interarticular membranes intact. The muscles in the femur were transected as distally as possible, and those in the patella were loosened at their origin. The same procedure was carried out in the tibio-metatarsal joint, and in neither case did extension occur. In fact, the joint remained in precisely that position in which it was manually placed. The legs from spiders of a number of different genera were used, and in all instances these results were observed. It is obvious, therefore, that the membranes themselves have little if any elasticity. This would certainly appear to render untenable any theory basing either extension or flexion on an inherent elasticity of the interarticular membranes.

C. *The effects of electrical stimulation*

In the following experiments the leg was removed at the trochanter and was anchored at the femur to the stage of a binocular dissecting microscope with plasticine. In most instances the tip of the tarsus was attached to a very lightly weighted heart lever by a length of silk thread, and the movements were recorded on a smoked kymograph drum. Stimulation was produced with micromanipulated platinum electrodes using a DuBois-Reymond inductorium.

Various ways of stimulating were used in an effort to produce extensor movements. The nerve was prepared in the femur and was stimulated either in its entirety or in bundles after splitting the nerve with a fine needle. In some instances the tendons of the flexor muscles were cut prior to stimulation of the nerve. In all instances, however, stimulation with currents of ordinary intensity resulted only in flexor contractions if any response was obtained. This supports the finding that no extensor muscles are present.

The functions of the respective muscles in the segments of the leg distal to and including the femur have been investigated by selectively stimulating each of the

muscles. Most of these studies were made on the walking legs of tarantulas, although some observations have been made on the legs of *Agelena naevia, Latrodectus mactans,* and *Miranda aurantia.* No differences between the species were found.

The leg was opened with a pair of small scissors and the chitin from the side opposite the muscle to be examined was removed with a pair of fine forceps. Small platinum electrodes mounted in Zeiss micromanipulators were then applied to the muscle with the aid of a dissecting microscope. Contraction of the muscle was ob-
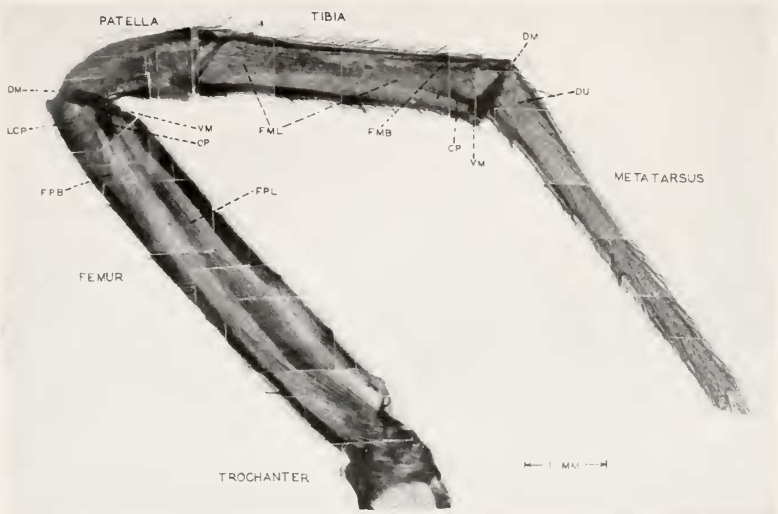

FIGURE 1. Composite photomicrograph of the mid-sagittal section of a walking leg of *Miranda aurantia.* CP = chitinous plate, DM = dorsal interarticular membrane, DU = depressor unguium muscle, FMB = flexor metatarsi bilobatus, FML = flexor metatarsi longus, FPB = flexor patellae bilobatus, FPL = flexor patellae longus, LCP = levator of chitinous plate, VM = ventral interarticular membrane.

served under the microscope to prove the selectivity of stimulation and movements of the parts of the leg were observed visually.

The muscles of the femur showed the following functions: The *flexor patellae bilobatus* (Fig. 1 fpb) produced strong flexion of the femoro-patellar joint. As Petrunkevitch (1909) and Brown (1939) reported, this bitendonous muscle lies laterally and dorsally in the femur, arising from the dorsal femoral surface and inserting directly on the proximal lip of the patella. The *flexor patellae longus* (Fig. 1 fpl), arising from the ventro-lateral lip of the trochanter and from the ventral proximal portion of the femur, extends ventrally and medially the full length of the femur, inserting, not on the proximal lip of the patella as has been described

(Petrunkevitch, 1909), but on the proximal margin of a chitinous horseshoe-shaped plate to whose distal margin are attached the proximal and distal portions of the ventral interarticular membrane (Fig. 3 cp). Stimulation of either of the bellies of this muscle likewise resulted in a flexor movement, although of considerably less intensity than that of the *flexor patellae bilobatus*.

An homologous picture was found in the tibia; the strongest flexor movement was obtained from stimulation of the *flexor metatarsi bilobatus* (Fig. 1 fmb), while the movements resulting from stimulation of the *flexor metatarsi longus* (Fig. 1 fml), although also flexor in nature, were much weaker than those of the former muscle.

Stimulation of the *depressor unguium* (Fig. 1 du) in the tibia, of the *levator unguium* in the metatarsus, and of the two main muscles in the patella gave the expected results, i.e., depression and elevation of the claw and the respective lateral movements of the tibia.

It has thus been possible to confirm most of the morphological findings of Petrunkevitch (1909) and Brown (1939), and to establish at the same time a clear functional proof of the specific activities of most of the muscles in the spider leg.

It was observed that "closed-leg" preparations, i.e., those in which the electrodes were inserted through the chitin of the femur, gave extensor movements of the two joints under consideration when stimulated very strongly for several seconds (coil distance = 3 to 1½ cm.). Upon removing the tip of the tarsus, however, such stimulation resulted in a much less pronounced extensor movement and was accompanied by the appearance of a growing droplet of blood at the severed end. Sealing the tip with plasticine resulted in a restoration of extensor movements of the original height. This stimulation was of such intensity that bubbles of hydrogen and oxygen appeared on the electrodes, and it is likely that the accumulation of gases was instrumental in producing the extensor movements.

D. *The possibility of an hydraulic extensor mechanism*

If the liberation of gases by electrolysis is sufficient to so increase the internal pressure of the leg that a straightening of the appendage occurs, it would seem quite feasible to consider that increases in the fluid pressure within the leg could result in extension. That such an increase does result in an extensor movement can be shown by gently squeezing an isolated leg. Extension occurs at the joints with a ballooning of the ventral interarticular membrane. Gaubert (1892) reported the phenomenon and considered it indicative of an extensor mechanism accessory to the "extensor muscle" which he firmly believed to exist.

Injection of fluid with a hypodermic syringe into any part of the leg, whether isolated or on the living or dead animal, is accompanied by extension of all parts distal and proximal to the point of injection. Injection into the abdomen or cephalothorax also produces extension of the appendages. The pressure necessary for producing this effect is small, a very light touch on the plunger of the syringe being sufficient to produce extension. Petrunkevitch (1910), although not mentioning the possibility of an hydraulic extensor mechanism, observed the above phenomenon, and used it as an indication of the completeness of injection while studying the circulatory system of spiders. He said, "Die Injektion musz so lange fortgesetzt werden, bis alle Beine straff auseinandergespreizt bleiben und die

Stacheln an ihnen nahezu senkrecht abstehen." Ten Cate (1931) showed that in Celaenia cutting off the abdomen resulted in stretching of the legs, but once the abdomen had been removed, the animal fell down as in death, i.e., the legs were flexed and no further extensor movements occurred. It would appear obvious that the constriction during the cutting process would momentarily increase the pressure giving rise to the extensor response.

That such hydraulic extension can be brought about mechanically does not give sufficient grounds, however, for assuming that the same mechanism is involved in the normal extensor movements of the live animal. The following experiments were therefore undertaken in an effort to see whether or not any similar pressure changes normally occur.

In the intact tarantula cutting off the tip of a leg produces a condition in which that leg is not extended upon stimulation of the animal in a manner which normally results in extension of the appendages, i.e., holding the animal in an inverted position. Sealing the tip restores the extensor function. The same effect has been obtained by opening the chitin of the femur in the intact spider. In such an animal pressure applied distal to the opening results in extension of the two joints, but pressure applied proximal to the opening results only in a marked effusion of fluid from the hole. Moreover, so long as the hole is open, the animal moves around with the operated leg in a flexed position, whereas the unoperated legs show normal extensor activity. The same result was obtained in *Agelena nacvia*.

Internal fluid pressure. Spiders always appear to be maintaining a high internal pressure within their bodies and appendages, as is seen by the fact that even a small perforation of the chitin of any living spider results in a great loss of blood whether the hole be in the abdomen, cephalothorax or appendage. In order to investigate the effect of lowering this internal fluid pressure, a number of tarantulas were dehydrated by keeping them for several weeks without water. They showed, prior to death, a condition in which walking was not accompanied by extension of either the femoro-patellar or tibio-metatarsal joints, and the spiders walked with their legs in a more or less markedly flexed position. In such an animal (tarantula) injection of 2 ml. of a salt solution [2] was accompanied by a period in which the two above-mentioned joints were extended as readily as in the normal animal. It should be recalled, however, that any perforation is accompanied by a considerable loss of blood, and upon removal of the injection needle from the abdomen, the animal bled profusely and in a short time again lost the ability to extend the legs. A second injection of physiological solution restored the normal condition, and when the hole was closed with collodion the animal ran about the cage in a more normal way, making use of its extensor mechanism.

The blood volume of the spider has also been lowered experimentally by withdrawing an appreciable amount of blood, using a small hypodermic needle, whereupon extension became markedly slower and less effective. Replacing the withdrawn blood with physiological solution gave a return of quick extensor movements of normal magnitude.

[2] Frog Ringers and several other salt solutions were unsatisfactory. Since these solutions had a molar concentration considerably lower than that of the physiological solution for crayfish described by van Harreveld (1936), the latter fluid was tried. It proved to be quite satisfactory, the animal remaining alive for somewhat longer than one hour following injection.

It has been pointed out that spiders characteristically die with their legs in a strongly flexed position. An interesting exception to this rule was observed in the case of a male tarantula which fell into its dish of drinking water and drowned. In this animal the legs were almost fully extended. Furthermore, the slightest pressure applied to the abdomen was sufficient not only to extend the legs maximally, but to raise the spines as well. It is evident that the spider in this case had imbibed water to such an extent that an abnormally high fluid pressure was present.

From the foregoing experiments the conclusion can be drawn that the internal fluid pressure of the spider must be kept high if maximum extensor activity is to be maintained.

Cardiac pulsations in the leg. Plateau (1887) and Gaubert (1892) observed that when spiders are suspended so that one or more of the legs is without a point of rest, those legs successively extend and flex through a small arc synchronously with the systolic and diastolic phases of the heart beat. Willem and Bastert (1918) and Willem (1920) made use of this movement of the tarsi to record changes in the cardiac rhythm when the spider was stimulated by various means, e.g., shining a bright light in the eyes of the animal. They showed that these flexor-extensor movements of the tarsi were more rapid during systole (extension) than during diastole (flexion), and that these movements could thus be considered to be a true picture of the sequences of cardiac pulsation. It has been possible to confirm this synchronization of rhythmic leg movements with the heart beat in the crab-spider, *Misumena alcatoria,* in which the movement of the dorsal chitin of the abdomen with each heart beat is conspicuous. Only the femoro-patellar and tibio-metatarsal joints showed the above phenomenon, and the ventral thin-walled sac at each of these joints showed ballooning with the extensor phase of each movement.

The experimental evidence which has been presented indicates that extension in spiders is intimately associated with the internal hydraulic pressure of the leg, which is in turn associated with the blood volume within the appendage. It also seems likely, although not certain, that the claws are spread apart by an increase of hydrostatic pressure. They are pulled together, however, by muscular action, and elevated and depressed by contraction of the appropriate muscles. For the complex movements of the male copulatory apparatus Osterloh (1922) has presented evidence that an hydraulic mechanism is present.

The details of the hydraulic mechanism are not obvious. An increase in the internal fluid pressure could be obtained in several ways. (1) The venous return pathway could be partially blocked, thereby permitting a greater volume of blood to accumulate in the appendage. Some mechanism of this sort must be present, or it becomes difficult to account for the fact that fluid is not forced out of the proximal end of an isolated leg upon compression of the femur. (2) The arterial flow of blood into the leg could be diverted from its normal path so as to produce an effective extensor thrust by ballooning the ventral interarticular membranes. A combination of these mechanisms may be involved.

There are, however, certain peculiarities of structure which have been observed in the two joints in which this type of extensor control is found. These should be considered as to possible roles in extension.

Structural peculiarities. From the ventral tibio-metatarsal and femoro-patellar interarticular membranes arise chitinous plates (one in each joint) which extend

proximally for a short distance. These plates are flattened dorso-ventrally and are bowed proximad. The plate in the femoropatellar joint was described by Gaubert (1892) but its presence has been consistently ignored by subsequent investigators, and the homologous structure in the tibio-metatarsal joint has apparently never been reported. From the proximal margin of these plates arise the tendonous strands whereby the *flexor metatarsi longi* and *flexor patellae longi* are respectively inserted. Moreover, a few isolated muscle fibers, arising from the distal dorsal wall of the femur and inserting on the dorsal surface of the chitinous plate (Fig. 2 lcp), seem to be uniformly present in sagittally cut preparations.[3] It was first thought that these fibers might be artifacts resulting from the cutting procedure, but care was taken to make the cut from different directions with respect to
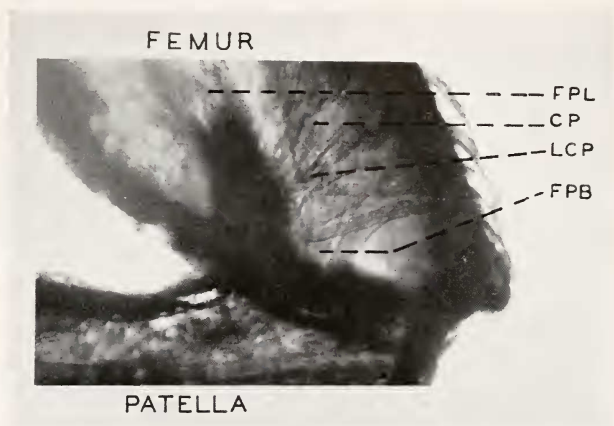
FIGURE 2. Photomicrograph of the femoro-patellar joint of *Miranda aurantia*. (Mid-sagittal section.) CP = chitinous plate, FPB = flexor patellae bilobatus, FPL = flexor patellae longus, LCP = levator of chitinous plate.

the femoro-patellar joint, and in all cases these fibers were found to lie in almost identically the same position on the dorso-ventral median line of the femur. It appears, therefore, that these few fibers form an heretofore undescribed muscle, the function of which is obviously elevation of the chitinous plate. It is probable that this group of fibers has been overlooked because they run in nearly the same direction as the more laterally located distal fibers of the *flexor patellae bilobatus*. Careful examination of Figure 2 will show, however, that these fibers of the large flexor muscle insert on the chitinous lip of the patella, not on the plate. The existence of

[3] The above sagittal preparations were made by first fixing the isolated leg in Petrunkevitch's (1933) copper-tri-nitro-phenol, dehydrating with graded alcohols and xylol, and imbedding in paraffin. The paraffin block was then trimmed under the dissecting microscope with a sharp scalpel until the mid-sagittal plane was reached. The excess paraffin was removed in xylol, the half-leg washed through several fresh xylol baths, and finally mounted in balsam.

an homologous group of fibers elevating the chitinous plate in the tibio-metatarsal joint is still uncertain.

The distribution of the arteries into the muscles and other tissues of the leg has never been adequately described. Causard (1896) figured the pedal arteries as simple uninterrupted tubes, one in each leg, emptying into the cavity of the leg through a single perforation in each segment except the tarsus where the artery ends as an open tube. Petrunkevitch (1910) stated that it is possible to trace the pedal arteries as far as the claw, but said nothing concerning any branching within the leg. Profuse branching of the main pedal artery occurs, however, as can be seen by injecting an animal with a colored latex medium.[4, 5] The branches arborize into the muscles in a manner quite similar to that described by Causard (1896) for the muscles of the cephalothorax (Fig. 3).
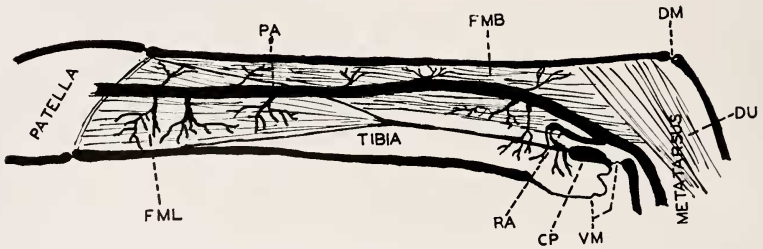
FIGURE 3. Diagram showing the vascularization in the tibia of a spider. CP = chitinous plate, DM = dorsal interarticular membrane, DU = depressor unguium, FMB = flexor metatarsi bilobatus, FML = flexor metatarsi longus, PA = main pedal artery, RA = reflected arterial branch, VM = ventral interarticular membrane.

With respect to a possible structural relation between the distribution of these vessels and the extensor function in the two joints under discussion, two peculiarities should be described. (1) Careful examination of the distribution of the main arterial trunk in the appendage shows that, although it runs somewhat dorsally through the major part of the femur and tibia, on approaching the respective joints, it dips ventrally and passes in close proximity over the chitinous plate. (2) In several preparations of the legs of tarantulas, a rather large branch has been found

to arise from the main pedal artery just proximal to the plate in the tibio-metatarsal joint. This branch is first reflected in a proximal direction for a short distance, whereupon it dips ventrally, arborizing laterally into the tissues surrounding the membranous sac bounded by the ventral interarticular membrane (Fig. 3 ra).

This distribution suggests that a mechanism for extension might involve the partial closing off of the main arterial flow, thus diverting a greater amount of blood into the region of the membranous sac, ballooning the latter structure and producing extension. Such a mechanism would have the distinct advantage of selectivity, either the tibio-metatarsal or femoro-patellar joint being independently extensible.

In order to examine the role which the plate may play in this function a study of its movement during flexion and extension of the leg has been made. Such motion can be watched through the thin transparent ventral interarticular membrane. The observation has been made that during flexion of the femoro-patellar joint the chitinous plate remains close to the ventral membrane. This is to be ex- pected from the position of the attachments of the *flexor patellae longus* which, lying ventrally, pulls the plate in a horizontal plane. Because of the ballooning of the ventral interarticular membrane by the inflow of blood with each extensor movement it was not possible to determine whether the plate is pulled deeper during extension or whether this only appears to be so because of the ballooning effect. At any rate, one loses sight of the plate during extensor movements. That con- traction of the fibers which lift the plate occurs during extension can only be as- sumed, therefore, and their designation as an auxiliary extensor mechanism must await further investigation.

SUMMARY

The absence of extensor muscles in the legs of spiders presents the problem of accounting for the quick extensor movements characteristic of these animals. The theory that the "elasticity" of the interarticular membrane might be the means whereby this is accomplished has been shown to be untenable.

Experimental evidence has been presented showing that extension is intimately associated with changes in the volume of blood in the spider leg, i.e., with changes in the internal fluid pressure in the leg.

Certain structural peculiarities in the joints have been described, but the evi- dence is insufficient to permit evaluation of their possible roles in extension.

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